

THE PHYLOGENETIC POSITION OF *ECHMATOCRINUS BRACHIATUS*, A PROBABLE OCTOCORAL FROM THE BURGESS SHALE

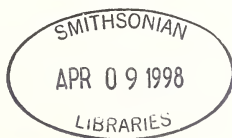
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ABSTRACT. The biological affinities of *Echmatocrinus brachiatus* Sprinkle, from the Burgess Shale (Middle Cambrian) of British Columbia, are re-evaluated based on study of all available material. This animal has an elongate, thinly plated/scaled body with a holdfast at one end and a calyx with eight(?) arms/tentacles at the other. Each of the latter bears alternating pinnule-like branches, and the pattern of the textured plating is very irregular, except for the uniserially plated arms/tentacles. Originally, *Echmatocrinus* was considered to be a crinoid, and recently it has been considered to be a cnidarian. The lack of any unequivocal echinoderm characters tends to discount the crinoid affinities of *Echmatocrinus*. Some characters suggest affinities with octocoral cnidarians, but, again, unequivocal affinity with cnidarians is lacking. However, the presence of eight arms/tentacles, an elongate conical body, and plating similar to living primnoid octocorals suggest that an octocoral affinity is more probable.

ECHMATOCRINUS brachiatus was considered by Sprinkle (1973, questionably), Sprinkle and Moore (1978), Sprinkle (1992), and Sprinkle and Collins (1995) to be the oldest representative of the class Crinoidea. Accordingly, it is an important organism for understanding the early history of echinoderms. The expectation is that it should provide guidance for identifying the echinoderms that were ancestral to crinoids and for polarizing characters for crinoid phylogenetic analyses. However, the unusual morphology of *Echmatocrinus* offers few clues to either the origin of crinoid characters or the origin of crinoids. For example, *Echmatocrinus* lacks a well-organized calyx with alternating rows of five plates and a four- or five-part column that are early Ordovician crinoid characters (Sprinkle, 1992).

The phylogenetic position of *Echmatocrinus* is re-examined critically for three reasons. Firstly, *Echmatocrinus* shares few morphological characters with Ordovician and younger Crinoidea. Secondly, no undisputed Cambrian crinoids are known. The oldest undisputed crinoids, of early Ordovician age, have no apparent close relationship to *Echmatocrinus*. Thirdly, the phylogenetic position of this fossil has recently become contentious. Conway Morris (1993a) assigned it to the Cnidaria, but Sprinkle and Collins (1995) argued that new material supports a crinoid interpretation. Re-evaluating the phylogenetic position of *Echmatocrinus* is essential before further progress can be made to understand the early evolution and classification of crinoids (Ausich and Babcock 1996).

Specimens are deposited at the Geological Survey of Canada, Ottawa, Ontario (GSC); the Royal Ontario Museum, Toronto, Ontario (ROM); and the U.S. National Museum, Smithsonian Institution, Washington, D.C. (USNM).



SYSTEMATIC PALAEOLOGY

Phylum CNIDARIA Hatschek, 1888
 Class ANTHOZOA Ehrenberg, 1834
 Order OCTOCORALLIA Haeckel, 1866
 Suborder INCERTAE SEDIS
 Superfamily INCERTAE SEDIS
 Family ECHMATOCRINIDAE Sprinkle, 1973
 Genus ECHMATOCRINUS Sprinkle, 1973

Type species. Echmatocrinus brachiatus Sprinkle, 1973.

Echmatocrinus brachiatus Sprinkle, 1973

Plate 1; Text-figure 1

- v*1973 *Echmatocrinus brachiatus* Sprinkle, p. 177, pls 42–43, text-figs 44–45.
 v.1975 *Echmatocrinus brachiatus*; Ubaghs, p. 91, fig. 7.
 v.1976 *Echmatocrinus brachiatus*; Sprinkle, p. 62, pl. 1, fig. 6.
 v.1977 *Echmatocrinus* Sprinkle, 1973 [sic]; Paul, fig. 3.18.
 1977 *Echmatocrinus brachiatus*; Webster, p. 75.
 1978 *Echmatocrinus brachiatus*; Ubaghs, pp. T275, T277, T280.
 v.1978 *Echmatocrinus brachiatus*; Sprinkle and Moore, p. T407, figs 219–220.
 1984 *Echmatocrinus brachiatus*; Smith, p. 455.
 v.1984 *Echmatocrinus brachiatus*; Paul and Smith, p. 458, figs 11, 19.
 1986 *Echmatocrinus brachiatus*; Webster, p. 133.
 1987 *Echmatocrinus brachiatus*; Broadhead, p. 179.
 v.1988 *Echmatocrinus brachiatus*; Broadhead, p. 257, fig. 20.1.
 1988 *Echmatocrinus brachiatus*; Ausich, p. 909.
 1988 *Echmatocrinus brachiatus*; Webster, p. 80.
 1988 *Echmatocrinus brachiatus*; Donovan, pp. 235, 239.
 1988 *Echmatocrinus brachiatus*; Smith, p. 811.
 v.1992 *Echmatocrinus brachiatus*; Sprinkle, fig. 2.
 1993a *Echmatocrinus brachiatus*; Conway Morris, p. 222.
 1993 *Echmatocrinus brachiatus*; Simms, p. 310.
 v.1994 *Echmatocrinus brachiatus*; Briggs, *et al.* p. 192, figs 156–157.
 1995 *Echmatocrinus brachiatus*; Sprinkle and Collins, p. 113.

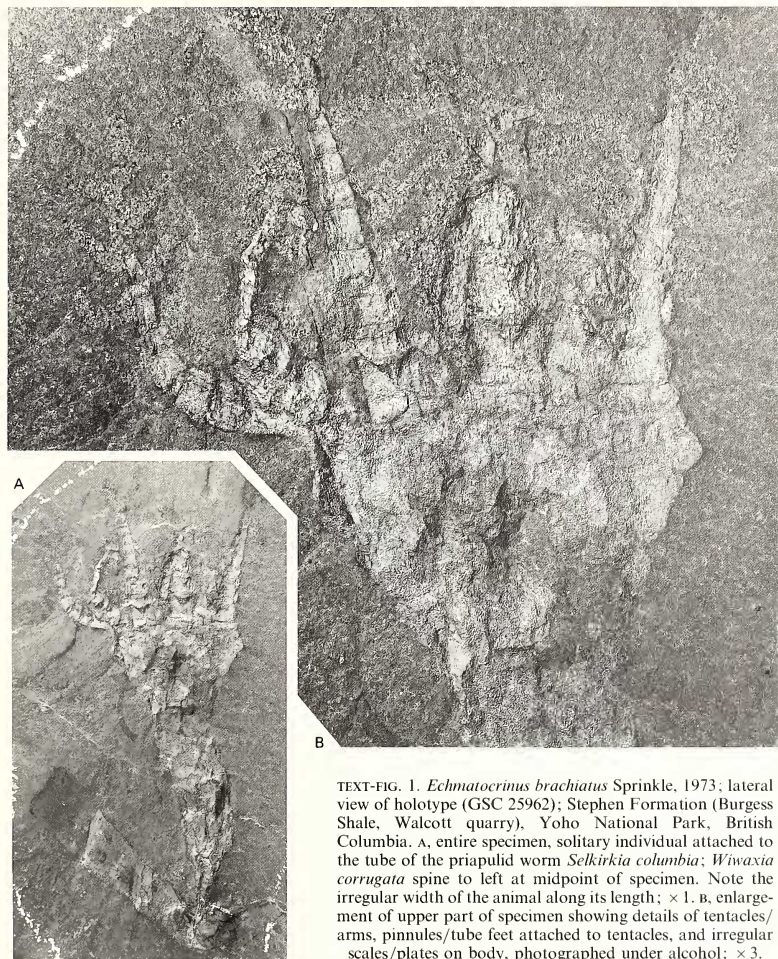
Material. The holotype is GSC 25962, and paratypes include USNM 165405 to 165408. Additional material includes ROM SWF (two slabs, several individuals), ROM RQ91.92-993 A and B (four individuals), ROM RQ9.7-92-976 A and B (three individuals), and ROM RQ10.1-92-1050 A and B (six individuals), ROM WT92-441 A and B, ROM WT 1167, USNM 165426, and questionably USNM 165427.

Occurrence. Stephen Formation (Middle Cambrian), Yoho National Park, British Columbia. Specimens have been collected from C. D. Walcott's quarry and P. E. Raymond's quarry at the Burgess Shale locality.

Diagnosis. Solitary octocoral with an elongate, conical body shape; covered with thin scales, irregularly shaped and arranged; body wall flexible; eight (possibly more) tentacles with uniserial scales, scales with a nodose and vermiform-ridged surface texture; body attached at a tapered base.

POTENTIAL ECHINODERM AFFINITIES

Sprinkle (1973, p. 178) identified the following features of *Echmatocrinus* as the keys to its interpretation: (1) plating of the calyx; (2) irregularly plated, elongate holdfast rather than a stalk with columnals; and (3) erect arms with uniserial segments and preserved tube feet. In their re-examination of *Echmatocrinus*, Sprinkle and Collins (1995) also emphasized: (1) the presence of



TEXT-FIG. 1. *Echnatocrinus brachiatus* Sprinkle, 1973; lateral view of holotype (GSC 25962); Stephen Formation (Burgess Shale, Walcott quarry), Yoho National Park, British Columbia. A, entire specimen, solitary individual attached to the tube of the priapulid worm *Selkirkia columbia*; *Wiwaxia corrugata* spine to left at midpoint of specimen. Note the irregular width of the animal along its length; $\times 1$. B, enlargement of upper part of specimen showing details of tentacles/arms, pinnules/tube feet attached to tentacles, and irregular scales/plates on body, photographed under alcohol; $\times 3$.

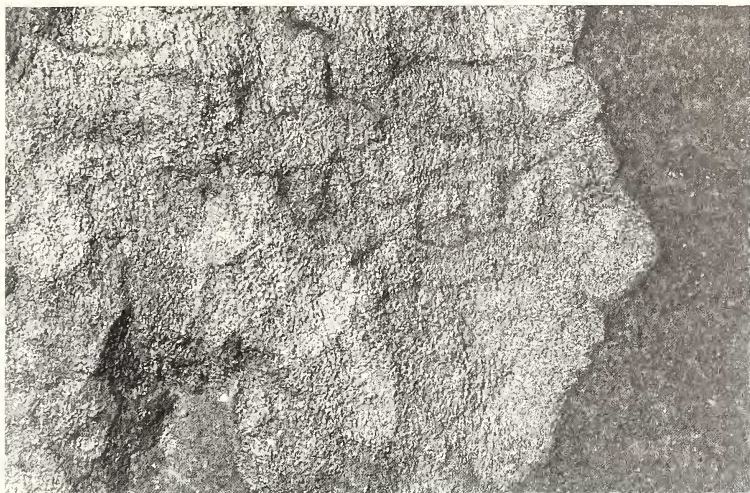
sutured plates; (2) reticulate surface ornament; and (3) possible ligament or muscle pads on arm ossicles. Additional critical attributes of these fossils include the composition and the inferred rigidity of the calyx.

The body wall

Sprinkle (1973) interpreted the body wall as being composed of irregular, polygonal, calcite plates. This implies that these plates had some thickness and that they abutted against adjacent plates. There is little indication that individual plates were imbricated and no indication of consistent imbrication (Text-fig. 1A). If plates were laterally abutting, *Echmatocrinus* plates should be hexagonal, as in most echinoderms. Examination of specimens indicates that the body wall was very thin (Sprinkle and Collins 1995), and preservational style indicates that it was not rigid. Indeed, specimens are commonly irregularly expanded along their lengths as a result of minor changes that occurred during burial and compaction (Text-fig. 1B). This preservational style is more characteristic of animals having thin body walls composed of weakly articulated sclerites than those with thick body walls and well articulated plates. The non-echinoderm nature of the body wall is especially evident if *Echmatocrinus* specimens are compared with undoubted Burgess Shale echinoderms such as eocrinoids (*Gogia radiata* Sprinkle) and edrioasteroids (*Walcottidiscus typicalis* Bassler and *W. magister* Bassler). *Gogia* and *Walcottidiscus* have distinct sutures between plates. In *Walcottidiscus* imbricate plating is well preserved. Although these edrioasteroid plates are thin, they appear to have been rigid, and the surface of the theca has distinct relief between the ambulacral and interambulacral areas. Normally, sutures between plates and junctions between adjacent plates are well defined in echinoderms, but in *Echmatocrinus* they are not (Pl. 1, fig. 2). Thecal plates of *Gogia* are preserved as moulds (e.g. in the Stephen Formation, USNM 165399; see Briggs *et al.* 1994, fig. 155). They are preserved in a similar way to those of other echinoderms having mouldic preservation; each plate mould has considerable relief and is clearly distinct from adjacent plates. Specimens of *Gogia* and other echinoderms from Cambrian deposits of Utah (e.g. Robison 1991; Sprinkle 1992) show that catastrophically buried specimens have distinct sutures. Specimens that have undergone slight disarticulation display equally or more distinct plate boundaries. In contrast, 'sutures' between plates are problematical on *Echmatocrinus*. Sprinkle and Collins (1995) described sutures as being darker in colour and depressed with slightly raised plate centres. After examination of all available material, we think that the existence of plate sutures is equivocal. Our observations indicate that in some cases, the 'sutures' are lower than the polygons that they separate, whereas in others they are higher. Under high magnification, the 'sutures' of the 'calyx' become considerably less distinct or almost disappear. Plate sutures of the 'stalk' are extremely difficult to discern (Text-fig. 1B). Only a small part of one specimen (ROM WT1167) is identified by us as preserving any strong indication of sutures between adjacent plates in any part of the animal other than the arms. Plate suture triple-junctions, typical of echinoderms with abutting plates, are nearly absent. On USNM 165405 and USNM 165408, areas on the calyx (not individual plates) look as though they are imbricated or torn and suggest a non-rigid, non-calcareous body wall. Commonly for any specimen, one 'plating' pattern is evident in high incident light, whereas other polygonal patterns are present in differing orientations of low incident light. Some patterns are hexagonal; most are not. A hint of plating regularity is present on USNM 165405 and USNM 165427 in which a portion of the body wall appears to be composed of hexagonal 'plates' arranged in spirals. However this arrangement is not definite. In summary, the plating of *Echmatocrinus* is highly irregular, at best, with plates abutting in some places and perhaps imbricating with others. A final,

EXPLANATION OF PLATE 1

Figs 1–2. *Echmatocrinus brachiatus* Sprinkle, 1973; lateral view of holotype (GSC 25962); Stephen Formation (Burgess Shale, Walcott quarry), Yoho National Park, British Columbia; note irregular scales/plates on body and character of texture on scales/plates interpreted as surface texture rather than stereomic microstructure. 1, enlargement of upper part of specimen immediately below the tentacles/arms. 2, enlargement in middle of the body. Both photographed under alcohol; $\times 9$.



1



2

important point is that no plates on *Echmatocrinus* can be identified as homologous to specific plates on any younger crinoid.

Holdfast/stalk

No crinoid has a stalk similar to the irregular, multiplated structure of *Echmatocrinus*. Other echinoderms, such as the eocrinoid *Lepidocystis*, may have a similar structure, but they are clearly plated. Presence of a holdfast/stalk in *Echmatocrinus* does not preclude it from being a crinoid, but it is quite unlike that of all early Ordovician crinoids, even *Aethocrinus moorei* Ubahgs and *Ramseyocrinus cambriensis* (Hicks), which were compared to *Echmatocrinus* by Sprinkle (1973, p. 178).

Stereomic microstructure

The surface of *Echmatocrinus brachiatus* has a distinctive pattern that Sprinkle (1973) attributed to echinodermal stereomic microstructure. Sprinkle and Collins (1995) reported that this pattern is similar to that of the edrioasteroid *Walcottidiscus* and not similar to other metazoans. However, rather than being the interconnected, three-dimensional stereom unique to echinoderms, the body wall surface, upon close inspection, has nodes and a vermiform, ridged surface texture (Pl. 1, figs 1–2; see also Conway Morris 1993a, p. 222). Spacing of the nodes of this texture (on USNM 165405) is 0.097 to 0.161 mm. Although much needs to be learned about stereomic microstructure of crinoids and stereom spacing variability across the skeleton, its spacing on the outside of calyx plates in living crinoids is typically one to two orders of magnitude smaller than the surface pattern on *Echmatocrinus* (see Macurda and Meyer 1975).

On *Walcottidiscus typicalis* (USNM 90754) some plates preserve a poorly developed surface pattern similar to that on *Echmatocrinus*, as discussed by Sprinkle and Collins (1995). However, other plates on this specimen have a much finer, continuous pattern of circular holes and bars (spacing = 0.014–0.028 mm) that is identical to echinoderm stereom. This comparison further suggests that true echinoderm stereom is absent in *Echmatocrinus* and that the coarse surface texture on *Echmatocrinus* only mimics the surface ornamentation of *Walcottidiscus*. In summary, preserved *Echmatocrinus* plates lack pores or secondarily filled pores that would be expected in the endodermally secreted stereomic skeleton of an echinoderm. Instead, the 'plates' appear to be part of an ectodermic skeleton.

Arms/tentacles

The uniserial, erect arms/tentacles are the most crinoid-like feature on *Echmatocrinus* (Sprinkle 1973). These stand out in higher relief (Text-fig. 1B) than other parts of the animal and were apparently the most rigid parts of the body. An isolated uniserial arm/tentacle piece (USNM 165426) demonstrates that the arms/tentacles were segmented (see Sprinkle, 1973, pl. 43, fig. 8). Eight arms/tentacles are the most that we can definitely count on any specimen (Text-fig. 1A), although Sprinkle (1973, p. 177) listed the arm/tentacle number as 'At least 8 (and possibly as many as 10)...'; Sprinkle (1992) listed the number as six to ten; and Sprinkle and Collins (1995) listed the number as seven to ten. If the maximum number of arms/tentacles is less than ten, *Echmatocrinus* lacks the pentamerous symmetry characteristic of echinoderms.

Long (up to 4–6 mm), thin (1 mm at base), unsegmented, uncalcified branches are borne from the arms/tentacles in an alternating pattern, one per arm/tentacle segment (Text-fig. 1B). Sprinkle (1973) interpreted these as preserved tube feet. If this is correct, these are the only known examples of preserved crinoid tube feet (Meyer 1982, p. 31) in the fossil record. Exceptional preservation of non-mineralized remains is expected on Burgess Shale fossils, but other crinoid-bearing *Lagerstätten* lack tube feet preservation on crinoids (e.g. Solnhofen Limestone, Mazon Creek-type deposits). Hundreds of exceptionally preserved echinoderms have been collected from Burgess Shale-type deposits from the Cambrian of Utah (e.g. Robison 1991), and no specimens have preserved tube feet.

V-shaped indentations occur on the outside of the arm/tentacle plates of *Echmatocrinus* (Text-fig. 1b). Sprinkle and Collins (1995) interpreted these as possible ligament or muscle pads, but this presupposed that *Echmatocrinus* is an echinoderm. If it is a crinoid, 'muscle pads' are highly improbable, because muscles are not considered to have evolved as a connective tissue between opposing brachials in crinoid arms until the Devonian (Ausich and Baumiller 1993). If *Echmatocrinus* is an echinoderm, these could indicate ligamentary tissue.

POTENTIAL OCTOCORAL AFFINITIES

The fossil record of octocorals is quite poor compared with that of many other invertebrate groups; therefore, comparisons herein are confined to living octocorals. Fossil octocorals occur in *Lagerstätten*, such as Mazon Creek-type deposits (Oliver and Coates 1987). Frond-like fossils from the Cambrian (Conway Morris 1993b; Crimes 1995; Zhang and Babcock 1996) and the Neoproterozoic (Glaessner 1984; Fedonkin 1992) have been allied with octocorals by some (e.g. Jenkin 1992; Conway Morris 1993b) although this view is not uniformly held (e.g. see Seilacher 1989, 1992). In any case, fossil octocorals or putative octocorals are not known in enough detail to permit detailed comparison with *Echmatocrinus*. No pretence is made that *Echmatocrinus* is closely related to any particular living octocoral, but comparisons of morphological characteristics between *Echmatocrinus brachiatus* and a variety of living octocorals are made in order to consider the affinities of this organism.

Nearly all living octocorals are colonial. However, a solitary octocoral does exist (Bayer and Muzik 1976), and pseudo-solitary octocorals having a dominant autozooid are also known (Bayer 1973). This suggests that the earliest octocorals were solitary animals (Bayer 1973). Polyp shape of many octocorals is conical, and eight tentacles are present. Tentacles may be simple, dichotomously branched, or otherwise branched (e.g. *Umbellula*). Tentacles are pinnate in octocorals, a character that is homoplastic with the Echinodermata. The Primnoidae are living, deep-sea octocorals that have an outer body wall covered with abutting or imbricating scales. Examples include *Fanellia*, *Fannyella*, and *Perissogorgia* (see Bayer and Stefani 1988; Bayer 1990). In living octocorals, the scales tend to be arranged in vertical columns, and scales lack triple-junctions at most scale junctures. The body wall is flexible rather than rigid.

Among the primnoid octocorals, the calcareous plates have a variety of shapes, but not simple polygons. The surface sculpturing of plates is variable, but includes the following: vermiform raised ridges, irregular rough texture, irregular striae, fine nodes, coarse nodes, and combinations of these patterns (Bayer and Stefani 1988).

Plates of *Echmatocrinus brachiatus* resemble the scales of modern primnoid octocorals (Bayer 1990) both in gross and in detailed structure. *Echmatocrinus* plates have irregular outlines. At least on the stalk they tend to be arranged in columns, and the surface texture is similar. The composition of *Echmatocrinus* plates is not known, although their preservation is consistent with an original calcareous composition.

Tentacles are not commonly preserved on fossil cnidarians, although a number of examples are known from the Phanerozoic (e.g. Foster 1979; Oliver 1984; Stanley 1986; Oliver and Coates 1987). Cnidarians from the Burgess Shale, such as *Mackenzia* (Briggs and Conway Morris 1986; Briggs *et al.* 1994), have tentacles preserved in a manner very similar to the structures of *Echmatocrinus* that were previously considered to be tube feet (Sprinkle 1973). These narrow, short, variously curled and non-mineralized structures in *Echmatocrinus* are quite reasonably interpreted as pinnules or ramifications on octocoral tentacles.

INTERPRETATION AND CONCLUSIONS

Echmatocrinus brachiatus is an animal with the following characteristics: an elongate, conical, irregularly plated/scaled body with a holdfast on one end and eight (possibly more) arms/tentacles at the other (Text-fig. 1b). Arms/tentacles are plated, and a series of alternating pinnule-like soft

parts extend along the tentacles. The body wall was firm but non-rigid. The plates are roughly textured on the outer surface. Apparently the plates were lightly skeletonized and calcareous, but this is not known with certainty. Suggested affinities of this animal are with the crinoids (Sprinkle 1973; Sprinkle and Collins 1995) and the cnidarians (Conway Morris 1993a). Re-examination of all available material leads us to favour a cnidarian interpretation and to suggest that *Echmatocrinus brachiatus* is a primitive, solitary octocoral.

Because *Echmatocrinus* has been considered to be the oldest crinoid and because crinoid morphology has been polarized by comparison with *Echmatocrinus* by many authors, comparing characters of this fossil with crinoid synapomorphies may be tenuous. Instead, they are compared with inferred synapomorphies known from early Ordovician crinoids. These inferred synapomorphies or essential crinoid features include a definite pentamerous symmetry, a meric or holomeric column, clear differentiation between the column and the aboral cup, a calyx composed of separate sutured plates, aboral cup plates in discrete circlelets offset by 36° or nearly 36°, at least one calyx plate circlelet in a ray position, and erect uniserial arms. *Echmatocrinus* lacks all of these inferred synapomorphies except erect, uniserial arms, if the appendages on this fossil are arms as opposed to tentacles.

If *Echmatocrinus* is not a crinoid, could it be another echinoderm? Features that more traditionally would be considered echinoderm synapomorphies and that could be preserved in the fossil record include the water vascular system, calcareous endodermal plating, pentamerous symmetry, and stereomicrostructure. Alternatively, in the deuterostome phylogeny of Jefferies (1986), synapomorphies include the calcite skeleton with stereomicrostructure and dextrothetism for living echinoderms and chordates, and fixation and radial symmetry for echinoderms. In this scheme the single, unique preservable feature for echinoderms is an endoskeleton with stereomicrostructure.

Sprinkle (1973) based his crinoid interpretation, in part, on the assumption that the 'preserved tube feet' were a proxy for the water vascular system, that the plating was echinodermal, and that stereom was preserved. However, as argued above, the 'tube feet' of *Echmatocrinus* are equally likely to be pinnules on the tentacles of octocorals rather than a proxy for the water vascular system of echinoderms. *Echmatocrinus* has plating, but whether this is endodermal or ectodermal cannot be determined. Its plating is strikingly different in appearance from that of the sympatric echinoderms *Gogia* and *Walcottidiscus* which have either abutting or imbricated plating, although this does not exclude the possibility that *Echmatocrinus* plates were endodermal. The original mineralogy of *Echmatocrinus* plates is not preserved. However, *Echmatocrinus* is interpreted here as lacking stereomicrostructure. Stereomicrostructure is preserved in some Burgess Shale echinoderms, but it does not occur in *Echmatocrinus*. This argues against *Echmatocrinus* being any type of primitive stalked echinoderm.

Perceived similarities to crinoids, such as the elongate body attachment structure, and arms/tentacles, can also be argued as cnidarian in affinity. However, the striking similarity between plate architecture and arrangement of modern primnoid octocorals and the eight, pinnate arms/tentacles (the most that we have been able to count on any specimen) strongly argue for an octocoral interpretation.

Three slabs have connected clusters of *Echmatocrinus* specimens: ROM RQ91.92-993 A and B with four individuals, ROM RQ9.7-92-976 A and B with three individuals, and ROM RQ10.1-92-1050 A and B with six individuals. In all cases smaller specimens of varying sizes are attached to a single larger individual. In the latter two cases the largest specimen to which others are connected lacks arms/tentacles, but the characteristic surface texture of these larger individuals clearly identifies them as *Echmatocrinus*. This pattern of attachment can be interpreted in two ways. Either juvenile individuals attached to adults, or the smaller specimens are budded from the largest ones. Very different phylogenetic interpretations follow from these two alternatives. Unfortunately, the lack of preservational detail does not allow for the verification or rejection of either alternative.

In conclusion, we agree with Conway Morris (1993a) that *Echmatocrinus* is neither a crinoid nor an echinoderm. There are no absolute homologies between *Echmatocrinus* and either crinoids or

octocorals. However, on balance, the preserved characters of *Echmatocrinus* show greater morphological similarity to octocorals than to crinoids or any other echinoderm group.

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